

LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
TRUPANEA JONESI CURRAN (DIPTERA: TEPHRITIDAE) ON NATIVE
ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea jonesi* Curran is a multivoltine, florivorous fruit fly (Diptera: Tephritidae) infesting at least 104 species of host plants in 42 genera, eight tribes, and 17 subtribes in California and other western United States. Accordingly, this tephritid is the species most commonly reared from mature flower heads of native Asteraceae throughout California. Records for three new host genera and eight new host species are reported. The egg, first-, second- and third-instar larvae, and puparium are described and figured. The abdominal, lateral spiracular complex of the third instar consists of a spiracle and a single placoid sensillum and thus differs from other third instar *Trupanea* spp. reported to date. A subdorsal sensillum on the gnathocephalum is reported for the first time from the third instar of a *Trupanea*. The life cycle of *T. jonesi* in California is of the aggregative type. Eggs were laid in closed, preblossom flower heads through or between the overlapping phyllaries into or between the florets. First and second instars fed on the ovules and florets, while the third instars principally fed on the soft achenes. The receptacles of infested flower heads were scored (visibly abraided) by the mouth hooks or not depending in part on larval densities and host-plant species. Infested flower heads in samples from 10 different hosts contained an average of 1.7 ± 0.1 (\pm SE) (range, 1–15) puparia and an average total of 80 ± 2 (25–119) soft achenes/florets, of which an average of 7.3 ± 0.5 (range, 2–40) soft achenes/florets, or 16% (range, 1–15%), were damaged by larval feeding. Courtship and copulation behaviors are described, including a characteristic, unique wing display combining rapid wing hamation with supination by males approaching females. Male-male combat using mouthparts and legs also is described. Five species of Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. jonesi* as solitary, larval-pupal endoparasitoids: *Eurytoma obtusiventris* Gahan, *E. veronia* Bugbee (Eurytomidae), *Halticoptera* sp. (Pteromalidae), *Mesoplobus* sp. (Pteromalidae), and *Pteromalus* sp. (Pteromalidae) Other possible primary parasitoids or hyperparasitoids reared along with *T. jonesi* from mature flower heads were *Eupelmus* sp. (Eupelmidae), *Pachyneuron* sp. (Pteromalidae) and one, unidentified species each of Cynipidae and Eulophidae.

Key Words: Insecta, *Trupanea*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, mating behavior, flower-head feeding, host-plant range, parasitoids

Trupanea jonesi Curran (Diptera: Tephritidae) is the most common species of indigenous, nonfrugivorous fruit fly encountered in California, belonging itself to a genus which occurs worldwide and that is one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California (Foote

and Blanc 1963, Foote et al. 1993). However, being of little or no economic importance, most species of *Trupanea* remain little known (Foote 1960, Foote et al. 1993). Detailed life histories of six species of *Trupanea* from southern California have been published (Cavender and Goeden 1982; Goeden 1987, 1988; Goeden and Teerink 1997c; Headrick and Goeden 1991; Knio et al. 1996b), and the immature stages of four of these species also described (Cavender and Goeden 1982, Goeden and Teerink 1997c; Headrick and Goeden 1991, Knio et al. 1996a). This paper describes the life history of a seventh species, *T. jonesi*, and its immature stages.

MATERIALS AND METHODS

This study began in 1991 and was based in large part on dissections of selected subsamples of flower heads of Asteraceae infested by *T. jonesi* from among many samples collected annually throughout California in the manner described by Goeden (1985, 1992). One-liter samples of excised, immature and mature flower heads from known hosts potentially containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Fourteen eggs, 3 first-, 12 second-, and 7 third-instar larvae, and 3 puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium

alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired ($n = 16$) in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Munz (1974), as updated by Hickman (1993) and Bremer (1994); tephritid names and nomenclature follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996a) and Goeden and Teerink (1996a, b, c; 1997a, b, c) and our earlier works cited therein. Means \pm SE are used throughout this paper. Voucher specimens of *T. jonesi* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Trupanea jonesi* was described by Curran (1932) (as *Trypanea*) from a female holotype and three female paratypes reared from *Aster subspicatus* Nees van Esenbeck (as *douglasi*) at Corvallis, Oregon. Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the strikingly different, sexually dimorphic, wing patterns of the female and male.



Fig. 1. Egg of *Trupanea jonesi*: (A) habitus, pedicel to left; (B) egg pedicel.

Immature stages.—The third instar of *T. jonesi* was described and the anterior spiracle, cephalopharyngeal skeleton, last abdominal segment, and posterior stigmatic chamber were drawn by Phillips (1946). Otherwise, the eggs, first and second instars, and puparium heretofore have not been described nor illustrated.

Egg: Twenty-seven eggs of *T. jonesi* dissected from heads of *Aster integrifolius* Nuttall were white, opaque, smooth; elongate-ellipsoidal, 0.73 ± 0.006 (range, 0.65–0.80) mm long, 0.21 ± 0.002 (range, 0.17–0.23) mm wide, smoothly rounded at tapered basal end; pedicel 0.02 mm long (Fig. 1A), with a single row of aeropyles (Fig. 1B).

The egg of *T. jonesi* is similar in shape to the eggs of other *Trupanea* species pre-

viously described, larger in width and length than *T. californica* Malloch, similar in size to *T. imperfecta* (Coquillett) and *T. signata* Foote, and shorter than *T. conjuncta* (Adams), *T. bisetosa* (Coquillett) and *T. nigricornis* (Coquillett) (Goeden 1987, 1988; Headrick and Goeden 1991; Knio et al. 1996a; Goeden and Teerink 1997c). A single row of aeropyles circumscribes the pedicel of *T. nigricornis* and *T. signata*, but the aeropyles of the latter are subrectangular; whereas, *T. bisetosa* has 1–2 rows of larger, circular to irregularly rounded aeropyles (Knio et al. 1996a).

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly; minute acanthae circumscribe thoracic and abdominal intersegmental lines (Fig. 2A); gnathocephalon conical (Fig. 2B), rugose pads dorsally and laterally, rugose pads laterad of mouth lumen serrated on ventral margin (Fig. 2B-1, C-1); six verruciform sensilla posteriorad of rugose pads (Fig. 2B-2); dorsal sensory organ a single dome-shaped papilla (Fig. 2B-3, C-2); subdorsal sensillum laterad of dorsal sensory organ (Fig. 2C-3), anterior sensory lobe (Fig. 2B-4) bears terminal sensory organ (Fig. 2C-4), pit sensory organ (Fig. 2C-5), lateral sensory organ (Fig. 2C-6), and supralateral sensory organ (Fig. 2C-7); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 2C-8); mouth hooks tridentate (Fig. 2B-5, D-1); median oral lobe laterally flattened, tapering anteriorly (Fig. 2D-2); labial lobe attached to median oral lobe, with two pore sensilla (Fig. 2D-3); prothorax circumscribed anteriorly by minute acanthae (Fig. 2E-1), rugose pads (Fig. 2E-2) and verruciform sensilla (Fig. 2E-3); a single stelex sensillum located dorsomedially on prothorax (Fig. 2E-4); anterior thoracic spiracles on posterior margin of prothorax bear 3–4 rounded papillae (Fig. 2E-5); meso- and metathoracic lateral spiracular complexes consist of a spiracle, a stelex sensillum (Fig. 2E-6), and a single verruciform sensillum (Fig. 2E-7); abdominal lateral spiracular complex consists of a spiracle (Fig. 2F-1),

and placoid-type sensillum (Fig. 2F-2); caudal segment circumscribed by minute acanthae (Fig. 2G-1), and stelex sensilla in a 2-dorsal, 4-ventral arrangement (Fig. 2G-2); posterior spiracular plates, with three ovoid rimae, ca. 0.038 mm in length (Fig. 2G-3), and four interspiracular processes each with 3–6 branches, longest measuring 0.013 mm (Fig. 2G-4); intermediate sensory complex ventrad of posterior spiracular plates among the minute acanthae (Fig. 2G-5) consists of a medusoid sensillum (Fig. 2H-1), and a stelex sensillum (Fig. 2H-2).

Trupanea jonesi is similar in general appearance to other previously described species, i.e., *Trupanea californica* (Headrick and Goeden 1991), *T. bisetosa*, *T. nigricornis* (Knio et al. 1996a), and *T. signata* (Goeden and Teerink 1997c). Differences among the *Trupanea* species described to date are found in the abdominal lateral spiracular complex. This complex in *T. californica* includes a single verruciform sensillum; in *T. nigricornis*, two verruciform sensilla; in *T. jonesi*, a placoid sensillum; in *T. signata*, one verruciform sensillum and a placoid-type sensillum, and in *T. bisetosa*, two verruciform sensilla and a placoid-type sensillum (Headrick and Goeden 1991, Knio et al. 1996a, Goeden and Teerink 1997c). *Trupanea jonesi* is similar to *T. signata* and *T. nigricornis* in having 3–6 branches in the interspiracular processes (Knio et al. 1996a, Goeden and Teerink 1997c); whereas, *T. californica* and *T. bisetosa* possess 6–8 branches (Headrick and Goeden 1991, Knio et al. 1996a). Phillips (1946) described *T. jonesi* with bidentate mouth hooks and anterior thoracic spiracles having 10 papillae; however, we show that *T. jonesi* has tridentate mouth hooks and 3–4 papillae. Knio et al. (1996a) first reported the subdorsal sensillum in first instars of *T. bisetosa* and *T. nigricornis*; our report is the first to verify this sensillum in a third instar of *Trupanea*.

Second instar: White, cylindrical, tapering slightly anteriorly, rounded posteriorly; weakly defined minute acanthae circum-

scribe thoracic and abdominal intersegmental lines; gnathocephalon smooth, few rugose pads laterad of anterior sensory lobe (Fig. 3A-1); dorsal sensory organ a dome-shaped papilla (Fig. 3A-2, B-1); subdorsal sensillum laterad of dorsal sensory organ (Fig. 3B-2); anterior sensory organ bears all four sensory organs (Fig. 3A-3, B-3); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 3B-4); mouth hooks bidentate (Fig. 3C-1); median oral lobe laterally flattened, tapered anteriorly (Fig. 3C-2); prothorax circumscribed anteriorly by minute acanthae, rugose pads and verruciform sensilla; anterior thoracic spiracles consist of 3–4 papillae (Fig. 3D); lateral spiracular complexes were not seen; caudal segment circumscribed by minute acanthae and stelex sensilla (Fig. 3E-1); posterior spiracular plates consist of three ovoid rimae, ca 0.026 mm in length (Fig. 3E-2), and four interspiracular processes, each with 3–6 branches, longest measuring 0.015 mm (Fig. 3E-3); intermediate sensory complex (Fig. 3E-4) consists of a stelex sensillum (Fig. 3F-1) and a medusoid sensillum (Fig. 3F-2).

The second instar differs from the third instar in general habitus, being more cylindrical than barrel-shaped. The gnathocephalon has fewer rugose pads, none of which are serrated. The mouth hooks are bidentate, with the medial tooth being very reduced. The minute acanthae which circumscribe the intersegmental lines are less defined than in the third instar. Because of the wrinkled nature of the prepared specimens, the lateral spiracular complexes were not observed. The ovoid rimae of the second instar are slightly smaller in size than those of the third instar.

First instar: White, cylindrical, tapering slightly anteriorly, rounded posteriorly, 2–3 rows of minute acanthae circumscribe each intersegmental line; gnathocephalon smooth, lacking rugose pads (Fig. 4B); dorsal sensory organ a dome-shaped papilla (Fig. 4A-1, B-1); subdorsal sensillum laterad of dorsal sensory organ (Fig. 4A-2); anterior sen-

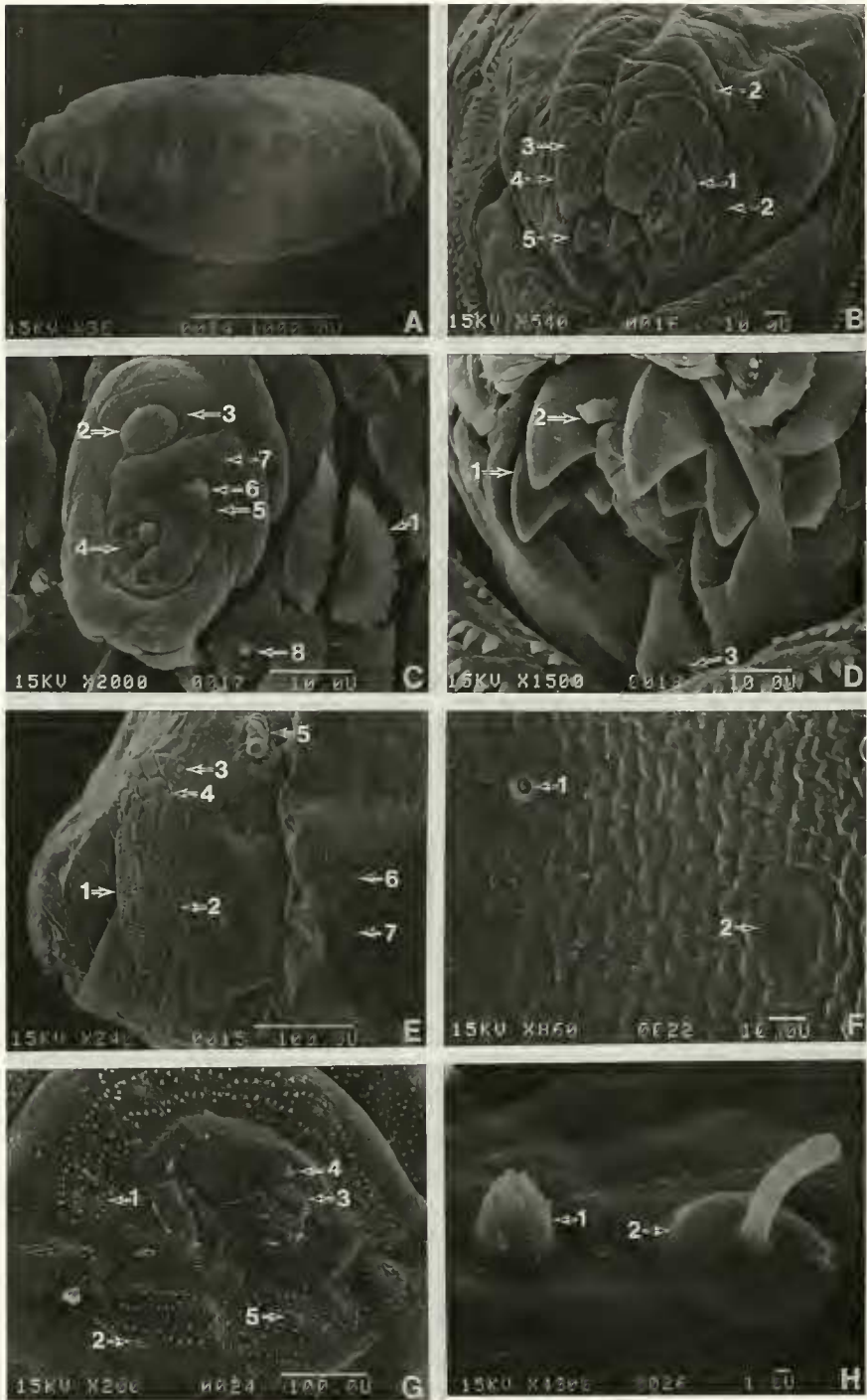


Fig. 2. Third instar of *Trupanea jonesi*: (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1—serrated rugose pads, 2—verruciform sensilla, 3—dorsal sensory organ, 4—anterior sensory lobe, 5—mouth hooks; (C) 1—serrated rugose pad: anterior sensory lobe, 2—dorsal sensory organ, 3—subdorsal sensory sensillum, 4—terminal sensory organ, 5—pit sensory organ, 6—lateral sensory organ, 7—supralateral sensory organ, 8—stomal sense organ; (D) gnathocephalon, ventral view, 1—mouth hooks, 2—median oral lobe, 3—

sory lobe bears all four sensory organs (Fig. 4A-3, B-2); stomal sense organs indistinct (Fig. 4B-3); mouth hooks bidentate (Fig. 4B-4); median oral lobe laterally flattened (Fig. 4B-5); labial lobe attached to median oral lobe, bears two pore sensilla; minute acanthae on ventral margin of prothorax; anterior thoracic spiracles not present; lateral spiracular complex not seen; caudal segment bears the posterior spiracular plates, posterior spiracular plates with two ovoid rimae, ca. 0.004 mm in length (Fig. 4C-1), and four rudimentary interspiracular processes (Fig. 4C-2).

The first instar differs from the previous two instars in lacking rugose pads on the gnathocephalon and the prothorax. There are also fewer minute acanthae circumscribing each intersegmental line. The dorsal, subdorsal and anterior sensory lobe sensilla are similar to the later instars, but the stomal sense organs are greatly reduced. Lateral spiracular complexes have been recorded for first instars of *Trupanea* spp. (Knio et al. 1996a), but because the *T. jonesi* specimens were wrinkled, these structures were not observed. First instar *T. jonesi* differs from *T. bisetosa* and *T. nigricornis* in having greatly reduced interspiracular processes (Knio et al. 1996a).

Puparium: Most puparia of *T. jonesi* are elongate-ellipsoidal (Fig. 5A), shiny black; anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment bears the posterior spiracular plates (Fig. 5C-1), a band of minute acanthae (Fig. 5C-2), and the intermediate sensory complex (Fig. 5C-3). Fifteen (4%) of 341 puparia dissected from flower heads (see below) were unpigmented medially (Fig. 5A, 6G). The 341 puparia averaged 2.76 ± 0.01 (range, 1.82–3.44)

mm in length; 1.26 ± 0.01 (range, 0.86–1.65) mm in width.

The puparia of *T. jonesi* are similar in size to *T. nigricornis*, larger than *T. californica* and *T. imperfecta*, and smaller than *T. bisetosa*, *T. conjuncta* and *T. signata* (Goeden 1987, 1988; Headrick and Goeden 1991; Knio et al. 1996a; Goeden and Teerink 1997c).

Distribution and Hosts

The distribution of *T. jonesi* mapped by Foote et al. (1993) included the western third of the U.S. north of Mexico and Canada, with this species recorded from several locations each in Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Utah, Washington, and Wyoming; from single locations in Iowa and Nebraska as well as from southern British Columbia.

Wasbauer (1972) and Goeden (1985, 1992) reported *T. jonesi* from eight tribes, 37 genera, and 86 species of Astereae in North America. Eight new rearing records for *T. jonesi* are listed below in the manner of Goeden (1992), that along with taxonomic changes in Hickman (1993) increase the reported host range to include eight tribes, 17 subtribes (Bremer 1994), 42 genera, and 104 species. All flies were reared from ca. 1-liter samples of mature flower heads from California.

New host genera.—*Chaetopappa*, *Orochaenactis*, *Syntrichopappus*

New host records.—*Artemisia rothrockii* Gray; 4 ♀; Horseshoe Meadow at 2870-m elevation, Inyo Nat. Forest, Inyo Co.; 14.ix.1993; *Chaetopappa aurea* (Nuttall) Keck; 1 ♂, 1 ♀; Spillway Canyon at 1400 m, San Bernardino Nat. Forest (S. Section), Riverside Co.; 21.v.1996; *Erigeron breweri*

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labial lobe sensilla; (E) gnathocephalon, prothorax, mesothorax, lateral view, 1—minute acanthae, 2—rugose pads, 3—verruciform sensilla, 4—stelex sensilla, 5—anterior thoracic spiracle, 6—stelex sensillum, 7—verruciform sensillum; (F) second abdominal segment, 1—spiracle, 2—placoid-type sensillum; (G) caudal segment, 1—minute acanthae, 2—stelex sensillum, 3—rima, 4—interspiracular process, 5—intermediate sensory complex; (H) intermediate sensory complex, 1—medusoid sensillum, 2—stelex sensillum.

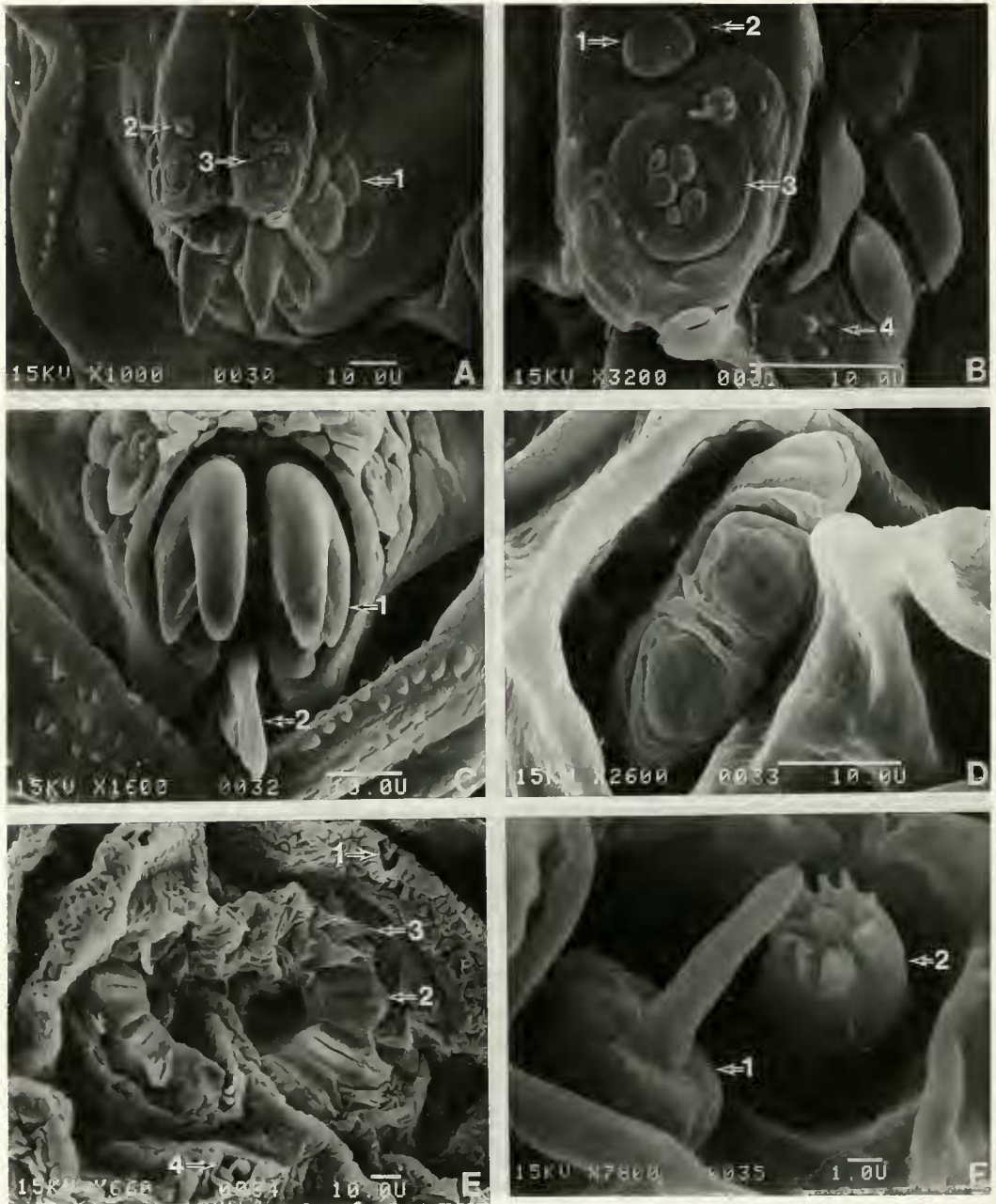


Fig. 3. Second instar of *Trupanea jonesi*: (A) gnathocephalon, anterior view, 1—rugose pads, 2—dorsal sensory organ, 3—anterior sensory lobe; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—sub-dorsal sensillum, 3—anterior sensory lobe, 4—stomal sense organ; (C) gnathocephalon, ventral view, 1—mouth hooks, 2—median oral lobe; (D) anterior thoracic spiracles; (E) caudal segment, 1—stelex sensillum, 2—rima, 3—interspiracular process, 4—intermediate sensory complex; (F) intermediate sensory complex, 1—stelex sensillum, 2—medusoid sensillum.

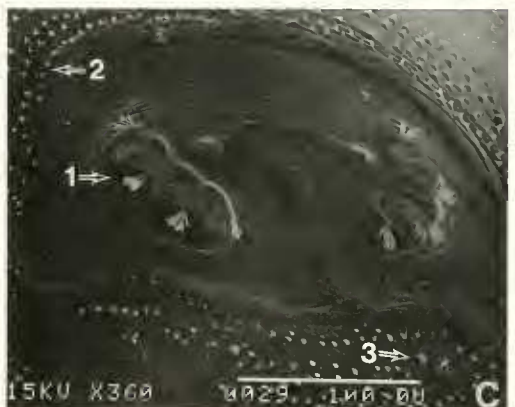
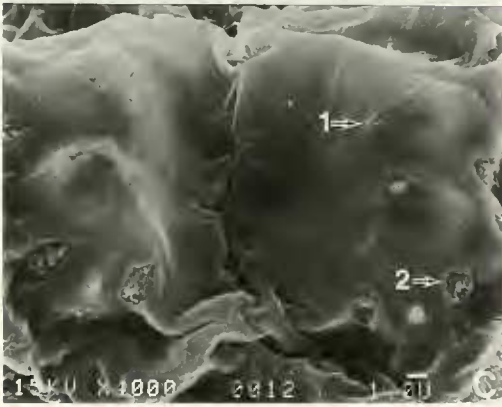


Fig. 4. First instar of *Trupanea jonesi*: (A) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—subdorsal sensillum, 3—anterior sensory lobe; (B) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hooks, 5—median oral lobe; (C) caudal segment, 1—rima, 2—interspiracular process.

Fig. 5. Puparium of *Trupanea signata*: (A) habitus, anterior end to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracles; (C) caudal end, 1—posterior spiracular plates, 2—minute acanthae, 3—intermediate sensory complex.

Gray; 2 ♂, 1 ♀; W of Carson Pass at 2470 m along St. Hwy. 88, Eldorado Nat. Forest, Alpine Co.; 18.viii.1993; *Orochaenactis thysanocarpha* (Gray) Coville; 1 ♂, 1 ♀; SE of Powell Meadow at 2440 m, Sequoia Nat. Forest (N Section), Tulare Co.; 15.vii.1993; *Senecio fremontii* Torrey and Gray; 1 ♀; 1 km S of Osa Mountain at 2610 m, Sequoia Nat. Forest (N. Section), Tulare Co.; 15.vii.1996; *S. hydrophilus* Nuttall; 1 ♂; Pimentel Meadows at 2210 m along St. Hwy. 395, Mono Co.; 18.viii.1993; *Syntrichopappus fremontii* Gray; 15 ♂, 18 ♀; N of Saddleback Butte at 927 m, W Mojave Desert, NW Los Angeles Co.; 16.iii.1996; *Tetradymia canescens* deCandolle; 1 ♂, 1 ♀; SW of Smith Mountain at 2440 m, Sequoia Nat. Forest (N Section), Tulare Co.; 14.vii.1993.

The host record for *Helenium hoopesii* Gray in Wasbauer (1972) was confirmed by us since publication of Goeden (1992). All 104 of the reported hosts of *T. jonesi* are from California, and all but 15 of these represent our or RDG's rearing records, including four from Wasbauer (1972) which we have confirmed to date. Thus, as previously noted, *T. jonesi* retains its distinction as having the broadest host range in terms of known genera and species attacked of any native tephritid from California, and from North America (Wasbauer 1972; Goeden 1985, 1992; Foote et al. 1993). Again, most hosts of *T. jonesi* in California belong to the Astereae, with good representation also in the tribes Helenieae, Heliantheae, and Senecioneae (Munz 1974, Hickman 1993, Bremer 1994). Similarly, the subtribes Asterinae, Chaenactidinae, Senecioninae, and Solidagininae of Bremer (1994) include the most host species.

Biology

Egg.—In 17 closed, preblossom, immature flower heads of *Aster integrifolius* Nuttall, eggs were inserted pedicel-last through the phyllaries, and deposited either parallel to the receptacle ($n = 15$, 88%; Fig. 6A), or perpendicular to it in two heads. In four

preblossom heads of *A. alpigenus* (Torrey and Gray) Gray, the long axes of single eggs lay perpendicular to the receptacle in two heads (Fig. 6B), or at 15° from the perpendicular in the other two heads. The passage of the aculeus was marked by small round punctures in the phyllaries (Fig. 6C). The diameters of the receptacles of 16 of these heads containing eggs averaged 2.9 ± 0.2 (range, 1.6–4.0) mm, and 21 such heads contained an average of 3 ± 0.4 (range, 1–6) eggs oviposited singly or side by side in pairs by one or more females. An average of 2.4 ± 0.5 (range, 1–5) ovules were damaged by an aculeus during oviposition in seven of these heads.

Larva.—Upon eclosion, first instars tunneled into and fed on the ovule and unelongated floral tube of a single floret, then moved into an adjacent, more centrally located floret. An average of 1.8 ± 0.3 (range, 1–6) first instars were found feeding within 21 closed, preblossom heads from *A. integrifolius* and *A. alpigenus*. The receptacles of these two *Aster* spp. averaged 3.9 ± 0.2 (range, 1.4–5.7) mm in diameter with an average of 70 ± 3 (range, 48–89) ovules/florets, of which an average of 4.6 ± 1.0 (range, 1–17) ovules/florets, or 6% (range, 1–28%), were damaged. Receptacles within these 21 infested flower heads were not scored (visibly abraided) by larval feeding.

Second instars fed mainly on ovules of preblossom flower heads or soft achenes of open heads, and usually at or near the centers of these flower heads (Fig. 6D). A few second instars were found at the margins of flower heads of *A. alpigenus* and *Helenium hoopesii* Gray (Fig. 6E). Again, neither seven, closed, preblossom flower heads of *A. alpigenus* nor six, open flower heads of *Chaenactis douglassii* (Hooker) Hooker and Arnott, averaging 4.2 ± 0.1 (range, 3.4–4.7) mm in diameter had receptacles that were scored by larval feeding (see below). These 13 flower heads contained an average of 1.5 ± 0.3 (range, 1–4) larvae that had destroyed an average of 3.3 ± 0.9 (range, 1–10) ovules/soft achenes, or 7.3% (range,

2.5–14.3%) of an average total of 47 ± 8.2 (range, 18–89) ovules/soft achenes in these infested flower heads.

Third instars confined their feeding to soft achenes or florets in the centers of open or postblossom heads, respectively (Fig. 6F). In 85 infested flower heads from 10 different host species averaging 3.8 ± 0.1 (range, 1.9–7.8) mm in diameter and containing an average of 1.4 ± 0.8 (range, 1–3) third instars (Fig. 6F), an average of 5.9 ± 0.5 (range 1–22) soft achenes/florets were damaged, or 15% (range, 2.2–76%). Most third instars fed with their long axes oriented perpendicular to, and mouthparts directed toward the receptacles, within the lower parts of the floral tubes and upper parts of the soft achenes, well above the receptacles. The receptacles were scored in only six (7%) of the 85 heads; i.e. in one of two infested heads of *Coreopsis californica* (Nuttall) H. K. Sharsmith; two of 31 (6%) heads of *A. integrifolius*; one of two heads of *H. hoopseii* (Fig. 6E); and three of four heads of *Chaenactis xanthiana* Gray. Three of the six heads with scored receptacles contained two or three larvae each, which suggests a positive trend toward receptacle scoring at higher larval density and a greater propensity for scoring within heads of certain hosts, for example, as reported among larvae of *Paracantha gentilis* Hering in flower heads of native *Cirsium* thistles (Headrick and Goeden 1990). (Receptacle scoring also is analyzed in greater detail below within heads containing puparia.) Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated.

Pupa.—Flower heads containing puparia (Fig. 6G, H) reflected the greatest amount of damage that the seed-feeding larvae of *T. jonesi* caused within heads of hosts sampled. Accordingly, 434 flower heads of 10 host species in six genera found to contain puparia were analyzed altogether, and by host genus and species (Table 1). The receptacles of infested flower heads of all 10

hosts averaged 4.4 ± 0.1 (range, 2.5–6.1) mm in diameter and bore an average total of 80 ± 2 (25–119) soft achenes/florets, of which an average of 7.3 ± 0.5 (range, 2–40) soft achenes/florets or 16% (range, 1–15%) were damaged. These heads contained an average of 1.7 ± 0.1 (range, 1–15) puparia. Most puparia of *T. jonesi* were found in the centers of the heads, all had their anterior ends facing away from the receptacles, and their long axes were perpendicular to the receptacles (Fig. 6G, H). *Trupanea jonesi* generally infested only a small proportion of the flower heads sampled and damaged only a small proportion of the immature achenes of the hosts listed in Table 1.

Receptacle scoring by *T. jonesi* larvae during feeding apparently was not obligatory, as it was absent in all infested flower heads of *Aster breweri* (Gray) Semple, *Chaenactis douglasii* (Hooker) Hooker and Arnott, *Chaenactis xanthiana* Gray, and *Layia glandulosa*; whereas, the receptacles of all 28 infested flower heads of *Coreopsis californica* examined were scored (Fig. 6G). The receptacles also were scored in three of 77 (4%) infested flower heads of *Arnica chamissonis* Lessing (Fig. 6H); three of four (75%) infested flower heads of *Aster alpigenus*; eight of 47 (17%) flower heads of *Aster integrifolius*; one of 29 (3%) infested flower heads of *Chaenactis fremontii* Gray; and nine (26%) of 35 infested flower heads of *Eriophyllum lanatum* (Pursh) Forbes. Two of three (66%) infested flower heads each of *Arnica chamissonis* and *Aster alpigenus*, six of eight (75%) flower heads of *Aster integrifolius*, and seven of eight (88%) with scored receptacles contained more than one puparia, which again suggests a positive correlation of larval densities and incidence of receptacle scoring (Headrick and Goeden 1990).

Adult.—The duration of the larval and pupal stages together approximated the duration of flower head development. Adults emerged from mature flower heads, and were long-lived under insectary conditions, as eight males averaged 63 ± 6 (range, 42–

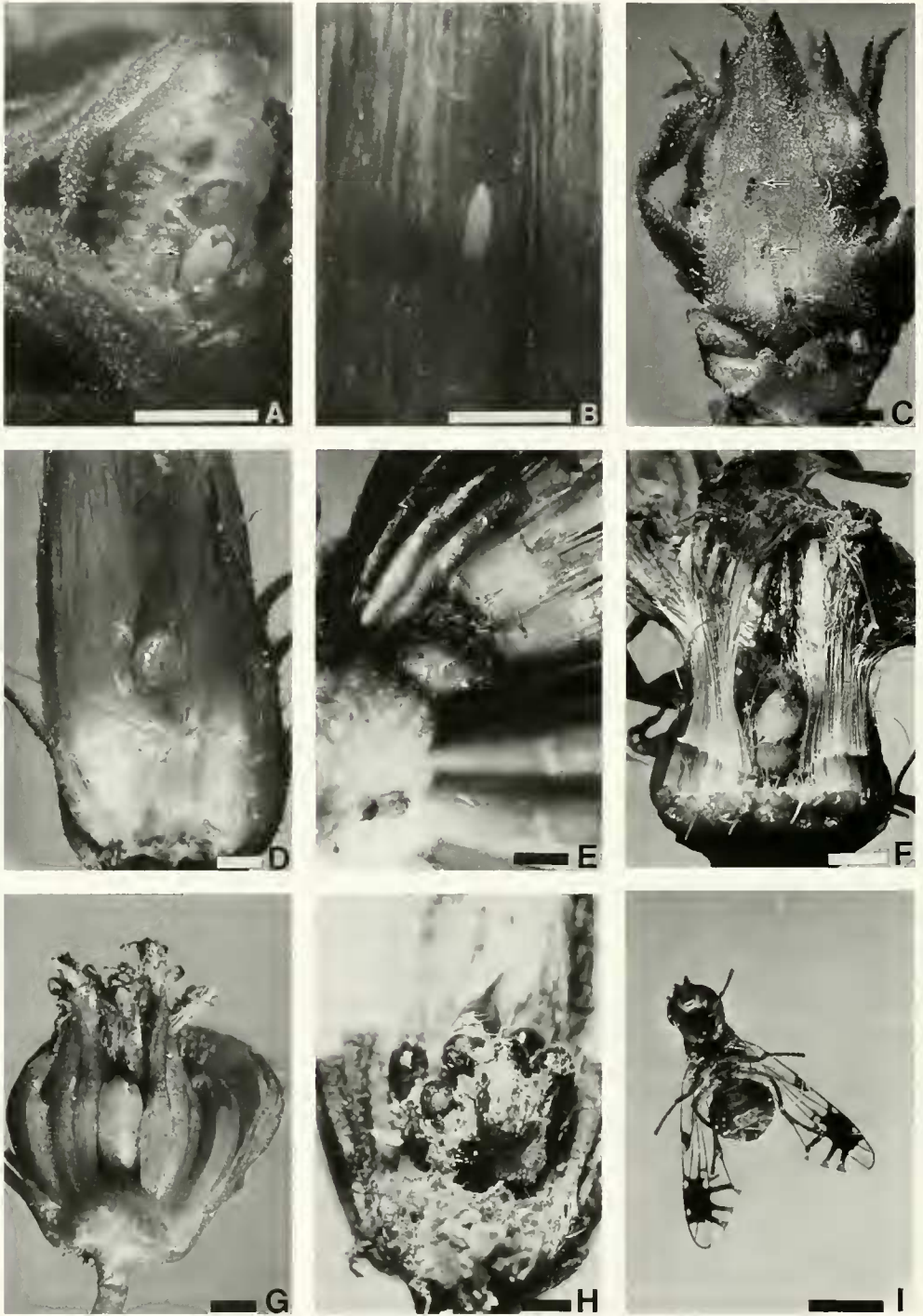


Fig. 6. Life stages of *Trupanea jonesi*: (A) pair of eggs (arrow) inserted in closed, preblossom flower head of *Aster integrifolius*, (B) egg inserted in central floret in flower head of *Aster alpigenus*, (C) ovipositional punctures (arrows) in phyllary of closed, preblossom, flower head of *A. integrifolius*, (D) second instar feeding on central floret in open head of *Aster breweri*, (E) second instar feeding on soft achene and scoring receptacle at margin of flower head of *Helenium hoopesii*, (F) two third instars in common, central, feeding cavity in

91) days, and 26 females averaged 76 ± 5 (range, 29–120) days.

Wing displays: Both sexes displayed synchronous and asynchronous supinations with vibrations (Headrick and Goeden 1994); however, their wing displays were imprecise and showed no observable rhythm. Males exhibited a unique hamation display during courtship (Headrick and Goeden 1994), which is described below.

Courtship: Male courtship displays were observed at all times throughout the day beginning at ca. 0700 h, and into the night under artificial lighting; however, adults were most active in the mornings. The abdominal pleura of males were distended for most of the display period (Fig. 61) concurrently with asynchronous wing displays. Males spent most of the display period upside down under the covers of arenas and visually tracking (facing toward) walking females.

Male courtship displays consisted of abdominal pleural distension and a unique wing display. Slow analysis with video-recording playback of this wing display was required to fully describe its components. As one wing was held over the dorsum the other wing was extended forward with supination up to ca. 90° , then the extended wing was brought back flat over the dorsum. As the first wing was brought back, the other wing was extended forward at exactly the same rate and distance, (= hamation), but with supination. The first wing was held over the dorsum until the second wing began to return, then the first wing was extended again and in time with the return of the second wing. This display increased in the arcs of extension and supination as the male moved closer to a female. This display was rapid such that the wing blades were blurred at normal viewing

speeds. The wing display climaxed as the male neared the female, his wings were held extended at 90° from the midline of the body, supinated 90° with respect to the substrate, but rapidly moved together, back-and-forth through only a few degrees. Then, the wing blades began to rise up and down in a plane parallel to the supinated blade and perpendicular to the substrate. If a female moved away from a displaying male, the intensity of the wing display diminished.

Males displayed hamation if they stood near a female and the intensity increased with proximity. If a female remained in place, a male moved toward her and attempted mounting. If she moved away, he followed her while raising his front legs and placing his tarsi onto her wings. If she still remained, he then climbed onto her dorsum, typically from behind ($n = 5$).

Copulatory induction behavior: A mounted male ceased his wing display and quickly grasped the female and began to drum his epandrium against the apex of her ovipositor. If the female was receptive, she exerted her aculeus and intromission was gained. If a female remained unreceptive and did not exert her aculeus, the mounted male used his front legs to drum on the top of her abdomen. Males remained on unreceptive females for up to ca. 10 min before dismounting. Unreceptive females used their hind legs to push at mounted males in attempting to dislodge them.

Copulation: In the final copulatory position, a male grasped the female with his front legs on top of her abdomen near her thorax, his middle legs around the middle of her abdomen with the tarsal claws hooked onto her pleura and his hind legs around her oviscapae with the tarsi pressed together beneath, or projected posteriad

Table 1. Achene feeding by larvae of *T. jonesi* in flower heads of native Asteraceae in southern California.

| Host-Plant Genera and Species Sampled | No. of Heads Dissected | No. (%) Heads Infested | Mean No. (Range) [%] ^a Achenes Damaged | Mean No. (Range) Total Achenes in Infested Heads |
|---|------------------------------|------------------------------|---|--|
| <i>Arnica chamissonis</i> | 448 | 90 (20.1%) | 7 (3-30) [10.3%] | 80 (25-119) |
| <i>Aster</i> spp. | 863 | 145 (16.8%) | 9 (2-40) [18.3%] | 54 (20-109) |
| <i>Aster alpigenuus</i> | 215 | 25 (11.6%) | 4 (2-8) [4.4%] | 86 (70-104) |
| <i>Aster breweri</i> | 148 | 9 (6.1%) | 4 (3-5) [17.9%] | 23 (21-25) |
| <i>Aster integrifolius</i> | 500 | 111 (22.2%) | 9 (2-28) [19.3%] | 50 (20-94) |
| <i>Chaenactis</i> spp. | 1000 | 129 (12.9%) | 6 (2-15) [16.1%] | 41 (16-82) |
| <i>C. douglasii</i> | 200 | 41 (20.1%) | 3 (2-5) [13.9%] | 23 (16-23) |
| <i>C. fremontii</i> | 600 | 48 (8%) | 8 (5-15) [15.9%] | 55 (30-82) |
| <i>C. xantiana</i> | 200 | 40 (20%) | 6 (2-12) [17.1%] | 36 (18-50) |
| <i>Coreopsis californica</i> | 600 | 28 (4.7%) | 5 (3-10) [14.7%] | 41 (15-60) |
| <i>Eriophyllum lanatum</i> | 200 | 35 (17.5%) | 11 (6-20) [22.5%] | 49 (35-70) |
| <i>Layia glandulosa</i> | 200 | 7 (3.5%) | 10 (3-19) [26.4%] | 42 (18-84) |

^a Mean % achenes damaged in all infested heads examined per host genus and species.

without touching the ovipositor. A mounted male displayed hamation as an agitation response to the female or to moving objects. His wings were typically held flat over his dorsum, with their costal margins parallel. The female's wings were spread at ca. 45°. Copulation lasted an average of 10 min (n = 5).

Before disengagement, a male pressed his hind tarsi against the apex of a female's ovipositor. Rubbing with the hind legs continued and became more vigorous as the termination of copulation neared. The male then turned and stepped off the female, moved behind her and walked away while quickly pulling the aedeagus from her aculeus. The aedeagus then was recoiled around the epandrium during grooming. Females moved away from the dismounted male and groomed while the aculeus was retracted. Males remained very active and the wing display changed from hamation to asynchronous supination.

After disengagement, males re-approached females with the abdominal pleura distended and displaying wing hamation. Females were observed to copulate only once with the same male while confined to arenas. Females also showed aggression toward males after copulation.

Male-male interactions: Two trials were conducted in which two males and a single

female were confined to an arena. Males interacted similarly to that observed with *Tepphritis stigmatica* and *Rhagoletis completa* (Boyce 1934, our unpublished data). A total of 11 interactions were recorded. Males faced each other and displayed synchronous supinations, during which the wings were held extended from the body at 100-110° and supinated ca. 90° with respect to the substrate. The males moved towards one another with their wings in this position. When they were within 2 mm, they raised up on their hind and middle legs and grappled with their front legs. During this upraised grapple, they fully extended their mouthparts and placed their labella together, holding onto each other with their front legs. The labella were pressed firmly together. In some battles, the mouthparts of the males were pressed together with such force that the labella slipped past each other and the heads of the two males knocked together, at which point both males immediately tried to place their labella together again (n = 2). Battling males also momentarily released their labella and rose completely vertically, venter to venter, with their front legs stretched above their heads and asynchronously boxing them. Then, they dropped down to the substrate and placed their mouthparts together again or they stopped and moved away from each

other with their wings still outstretched. As they moved away from each other, they switched to hamation displays. No male was observed to successfully copulate with a female after battling with another male. In one episode, two males faced each other with their wings extended 90° perpendicular to their bodies and to the substrate, then moved toward each other. One male grabbed onto the wings of the other with his front legs, inducing the latter male to pull away. The male gripped the wings firmly, but the other male was able to wrest free. They faced each other again and locked their mouthparts together and grappled with their front legs. They remained together for ca. 30 sec, then finally broke apart and began hamation displays again.

Seasonal history.—The life cycle of *T. jonesi* in southern California follows an aggregative pattern in which the long-lived adults in reproductive diapause overwinter (probably in riparian habitats) and aggregate to mate on preblossom host plants in late winter and early spring. They reproduce, at first in the low-elevation, Colorado (upper Sonoran) Desert, then in the high elevation Mojave Desert, interior valleys, and coastal areas (Headrick and Goeden 1994). Reproduction by subsequent generations of this multivoltine tephritid continues thereafter throughout the spring, summer, and fall on a wide range of alternate host plants, as flowering of Asteraceae continues at ever higher elevations and more northerly latitudes in California.

Natural enemies.—Five species of Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. jonesi* as solitary, larval-pupal endoparasitoids: *Eurytoma obtusiventris* Gahan, *E. veronia* Bugbee (Eurytomidae), *Halticoptera* sp. (Pteromalidae), *Mesoplobus* sp. (Pteromalidae), and *Pteromalus* sp. (Pteromalidae). Specimens similar to *E. obtusiventris* or *E. veronia*, and either variations or undescribed species, currently are under study by Michael Gates, Department of Entomology, University of California,

Riverside. Additional, possible primary parasitoids or hyperparasitoids reared from mature flower heads along with *T. jonesi* were identified as *Pachyneuron* sp. (Pteromalidae), *Syntomopus* sp. (Pteromalidae), *Eupelmus* sp. (Eupelmidae), and one, unidentified, apparent species each of Cynipidae and Eulophidae.

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